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BRIEF REPORT

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Wide divergence of fungal communities inhabiting rocks and soils in a hyper-arid Antarctic desert

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Abstract

Highly simplified microbial communities colonise rocks and soils of continental Antarctica ice-free deserts. These two habitats impose different selection pressures on organisms, yet the possible filtering effects on the diversity and composition of microbial communities have not hitherto been fully characterised. We hence compared fungal communities in rocks and soils in three localities of inner Victoria Land. We found low fungal diversity in both substrates, with a mean species richness of 28 across all samples, and significantly lower diversity in rocks than in soils. Rock and soil communities were strongly differentiated, with a multinomial species classification method identifying just three out of 328 taxa as generalists with no affinity for either substrate. Rocks were characterised by a higher abundance of lichen-forming fungi (typically *Buellia*, *Carbonea*, *Pleopsidium*, *Lecanora*, and *Lecidea*), possibly owing to the more protected environment and the porosity of rocks permitting photosynthetic activity. In contrast, soils were dominated by obligate yeasts (typically *Naganishia* and *Meyerozyma*), the abundances of which were correlated with edaphic factors, and the black yeast *Cryomyces*. Our study suggests that strong differences in selection pressures may account for the wide divergences of fungal communities in rocks and soils of inner Victoria Land.

INTRODUCTION

The extreme environmental conditions of continental Antarctic soils select for highly resistant fungi with peculiar cellular adaptations, such as the ability to synthesise cold-active enzymes and antifreeze proteins (Krishnan et al., 2011, 2018; Robinson, 2001; Zucconi et al., 2020). These fungi endure multiple combined stressors, such as frequent freeze–thaw cycles, scarcity of nutrients and bioavailable water, intense solar radiation, and often high salinity (Godinho et al., 2013). In continental Antarctica, and especially in the arid soils of the region, bacterial communities are relatively diverse (Cowan et al., 2014; Severgnini et al., 2021), whereas, in contrast, fungal alpha diversity is typically low (Pointing et al., 2009; Rao et al., 2012). Low fungal diversity in Antarctic environments is attributable to the strong filtering imposed by the stressors described above and the limited propagule dispersal of some fungi. Despite aerobiological surveys in coastal Antarctica suggesting that large numbers of viable cells and spores can be transported over long distances (Bottos et al., 2014; Duncan et al., 2010), the aerodispersion of fungi from other continents is limited (Archer et al., 2019), with the primary sources of propagules in continental Antarctica being local hotspots such as microbial mats associated with local water bodies (Cowan et al., 2014; Hopkins et al., 2009). In addition, it

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has been shown that endemic Antarctic fungal taxa are more likely to be metabolically active under extreme environmental conditions than cosmopolitan species that are present in soil (Cox et al., 2019). The broad metabolic capabilities of fungi are crucial for cycling scarce soil organic matter and, in the case of lichen mutualism, which provides nutrients for other life forms in severely oligotrophic Antarctic environments, for sustaining primary production (Onofri et al., 2007; Ruisi et al., 2007).

Despite the pivotal role of fungi in the Antarctic, studies on soil fungal diversity in continental Antarctica are still limited in comparison with those focused on bacterial communities (Bottos et al., 2014; Kim et al., 2015; Tytgat et al., 2016; Van Horn et al., 2014). Furthermore, previous studies of soil fungal diversity in Antarctica have typically been carried out using culturing methods (Arenz & Blanchette, 2011; Connell et al., 2008). Many recent studies using cutting-edge molecular techniques have been focused on the Maritime Antarctic (see for example, da Silva et al., 2020; Durán et al., 2019; Newsham et al., 2021, 2022; Rosa et al., 2020; Santos et al., 2020) or coastal sites in continental Antarctica (Canini et al., 2020; Ji et al., 2016; Siciliano et al., 2014), and with comparatively few studies using these techniques on inner continental Antarctic fungal communities. The handful of molecular mycological studies hitherto carried out in inner continental Antarctica have revealed the dominance of a narrow range of fungal taxa in soils, primarily belonging to Ascomycota and Basidiomycota, with the latter mainly being represented by yeasts (Arenz et al., 2014; Pudasaini et al., 2017; Wei et al., 2016). Most of the observed taxa have yet to be identified at high taxonomic resolution. Additionally, abiotic environmental factors, especially physicochemical soil parameters, appear to be the main predictors of the distribution of species recorded using molecular methods (Canini et al., 2020, 2021; Connell et al., 2006).

Rocks also provide suitable habitats for fungi and other microbes in continental Antarctica (Cary et al., 2010; Cowan et al., 2014; Nienow & Friedmann, 1993). The porous nature of the sandstone rocks that occur in the McMurdo Dry Valleys allows the ingress of water and the exchange with the atmosphere of gases close to rock surfaces, facilitating the photosynthesis of algae and cyanobacteria (Friedmann, 1982). Furthermore, the absorption of solar radiation during austral summer, which heats rock surfaces to >0°C (Kappen & Friedmann, 1983), leads to increased microbial activity (Friedmann et al., 1993). The microbial communities of the rocks are stratified, with outer layers a few millimetres below the rock surface dominated by darkly-pigmented fungal hyphae enveloping algal cells, deeper layers by hyaline hyphae, and the deepest layers by abundant algae and cyanobacteria (Friedmann, 1982; Zucconi et al., 2016). The latter form lichens with the fungi, which support the growth of other microorganisms by screening excessive solar radiation and increasing water and nutrient retention (Friedmann, 1982; Friedmann et al., 1993). Many studies have described the fungal composition of endolithic continental Antarctic communities, in particular that of lichen-dominated cryptoendolithic communities in the rock outcrops that dominate the region (e.g., de la Torre et al., 2003; Friedmann, 1982; Selbmann et al., 2005, 2017). These studies have highlighted the presence of both lichen-forming and free-living fungi, with a prevalence of Lecanoromycetes and Dothideomycetes (e.g., Archer et al., 2017; Coleine, Stajich, et al., 2018), as well as the influence of abiotic variables on fungal diversity and function (Coleine, Zucconi, et al., 2018). However, previous studies have not compared the diversity and taxonomic composition of fungal communities in rocks with those of surrounding soils in continental Antarctica.

The most obvious distinction between rocks and soils is related to their microenvironmental characteristics. Each substrate is subjected to strong environmental pressures, with, for example, higher water availability combined with lower desiccation and physical disturbance in rocks than in soil (Chan et al., 2013; Cowan et al., 2014; de los Ríos et al., 2007; Wei et al., 2016). Because of these buffered conditions, the endolithic environment favours lichen photosynthetic carbon fixation and carbohydrate metabolism (Cowan et al., 2014), making it an oasis of productivity (Pointing, 2016; Pointing & Belnap, 2012). As a consequence, cryptoendolithic communities are considered to be major sources of organic matter and microbial propagules in oligotrophic continental Antarctic ecosystems (Cary et al., 2010; Cowan et al., 2014; Cowan & Tow, 2004). Given the significant differences in microclimatic conditions between rocks and soil, it is surprising that the possible filtering effects imposed by the two environments on microbial communities have only been marginally explored in Antarctic deserts (Rego et al., 2019; Van Goethem et al., 2016). In addition, it is not known if microbial propagules are exchanged between rocks and soils, as might occur when rocks frequently shatter under freeze–thaw processes and are dispersed through the landscape by the strong winds that characterise the McMurdo Dry Valleys (Campbell & Claridge, 1987; Friedmann, 1982).

Here, we hypothesised that, despite the low fungal diversity in continental Antarctic deserts, rocks, and soils would strongly select for different fungal communities, possibly as a result of their different microclimatic conditions. To test this hypothesis, we collected rock and surrounding soil samples from different locations in a remote continental Antarctic desert and examined them for the potential presence of substrate-specific fungal taxa.

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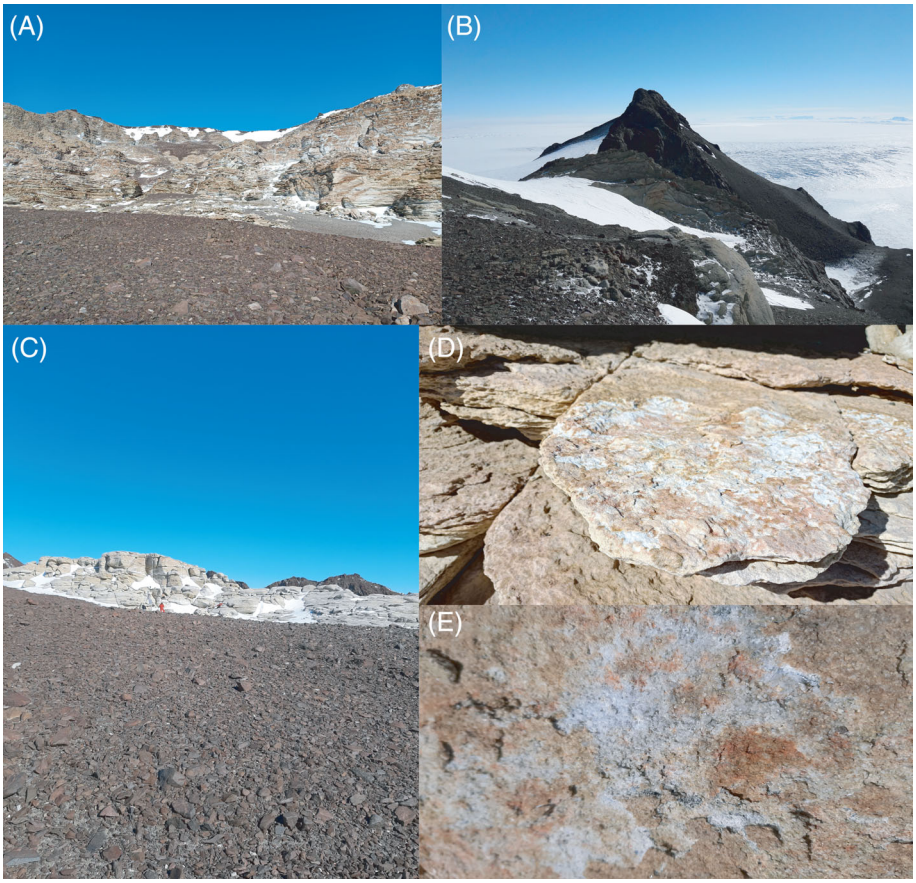

FIGURE 1 Landscapes at (A) Battleship Promontory, (B) Trio Nunatak, (C) Richard Nunatak, and details of exfoliated surfaces of colonised sandstone outcrops at (D) Battleship Promontory and (E) Trio Nunatak.

MATERIAL AND METHODS

Sampling and physicochemical parameters

Rock (sandstone) and surrounding soil samples were collected in the austral summer of 2018–2019 from three different localities in Victoria Land, namely Battleship Promontory, Trio Nunatak, and Richard Nunatak (Figure 1). At each location, a sandstone outcrop showing evident lithic colonisation was sampled in triplicate, with visibly colonised areas of rock (Figure 1D, E) being sampled immediately below the surface. Similarly, soils at 0, 50, and 100 m from each outcrop were collected in triplicate at 5–10 cm depth. All samples were collected using sterile utensils and were preserved in sterile bags at −20°C until laboratory analyses. An aliquot of each soil sample was also used for the determination of physicochemical parameters, viz., total carbon (C) and nitrogen (N), total and available phosphorus (P), moisture, pH, cation exchange capacity, the concentrations of the main exchangeable cations (Na^{+}, K^{+}, Ca^{2+}, and Mg^{2+}), and soil texture according to the standard methods of SISS (Società Italiana della Scienza del Suolo; Colombo & Miano, 2015).

DNA extraction and sequencing

Total DNA was extracted from 1 g of rock or soil samples using a DNeasy PowerSoil Kit (QIAGEN, Hilden, Germany), following the manufacturer's protocol. The ITS1 region was amplified using ITS1F (Gardes & Bruns, 1993) and ITS2 (White et al., 1990) primers, and libraries were prepared following the protocol of Smith and Peay (2014). Amplicons and/or good-quality libraries from soil samples collected at 0 m from Trio Nunatak rock outcrops could not be obtained. The equimolar pool of uniquely barcoded amplicons was paired-end sequenced (2 × 250 bp) on an Illumina MiSeq platform at Macrogen, Inc. (Seoul, South Korea).

Bioinformatic and statistical analyses

Bcl files were converted into Fastq files and demultiplexed using bcl2fastq (v 2.18). Demultiplexed sequences were processed with the Amplicon ToolKit (AMPtk) for NGS data (formally UFITS) v.1.3.0 (Palmer et al., 2018). The starting reads were subjected to quality trimming and PhiX screening via USEARCH with default parameters (v. 11.0.667; Edgar, 2010). Reads

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of <100 bp were removed, those of >250 bp were trimmed, and paired-end reads were merged in a single step. As recommended by recent studies (Kauserud, 2023; Tedersoo et al., 2022), the reads were clustered into operational taxonomic units (OTUs) at a 97% species identity threshold, using VSEARCH v 2.22.1 (Rognes et al., 2016), simultaneously removing putative chimaeras. Taxonomy was assigned manually to OTUs by comparing the results of analyses using the hybrid SINTAX/UTAX approach against a curated database that includes the full UNITE + INSD database (Edgar, 2010), and best hits in the BLAST database. Additionally, OTUs with uncertain assignments were also screened manually in BLAST considering all good quality hits. Rare OTUs (i.e., OTUs with <5 reads in the dataset) and OTUs with <70% identity to any known fungal sequence were excluded from downstream analyses. The OTU table obtained was normalised for the following statistical analyses by rarefying the number of reads per sample to the smallest library size (30,702 reads) using the *rrarefy* function in the *vegan* package v. 2.6-4 (Oksanen et al., 2022) in R v. 4.2.1 (R Core Team, 2018).

Differences in richness and Shannon diversity between rocks and soils, and between soils collected at 0, 50, and 100 m from outcrops, were tested with a Kruskal–Wallis test (McKight & Najab, 2010) followed by Dunn multiple comparisons (Dunn, 1964), with *p*-values adjusted using the Benjamini–Hochberg method. Beta dispersion was calculated for fungal OTUs to test if the groups had the same centroids and heterogeneity. Non-metric multidimensional scaling (NMDS) was used to visualise beta diversity. Permutational multivariate analysis of variance (PERMANOVA) was applied to assess drivers of beta diversity. The OTU table was centred log-ratio transformed to remove the compositional constraints from the taxonomic variables, and then the relationships between the most frequent OTUs in soil samples (occurring in at least 33% of the samples) and physicochemical parameters were tested using Pearson correlations (Aitchison, 1982). Linear discriminant analysis (LDA) effect size (LEfSe), based on LDA scores of >2 and *p*-values of <0.05, was used to characterise the fungal taxa associated with rock and soil (Segata et al., 2011). Cosmopolitan and specialist OTUs in rock and soil samples were determined using a multinomial species classification method (CLAM) using the 'vegan' package and the function 'clamtest' in R (Chazdon et al., 2011; Pedrinho et al., 2020). The differences in the distribution of the soil samples based on their physicochemical parameters were analysed by principal component analysis (PCA), performed with the 'prcomp' command in R.

RESULTS

From the initial 6,886,050 reads obtained, 6,051,905 valid reads were retained after quality filtering. Clustering, after chimaera removal, resulted in 1160 valid OTUs, corresponding to 4,692,229 reads mapped to OTUs (77.5% of the total). After removing rare OTUs, 977 OTUs were retained. Of these, 625 OTUs that had no match to fungal sequences in the databases were removed. The dataset consisted of 328 OTUs following rarefaction. Among these, 170 OTUs were present in only one sample and only two OTUs were present in >70% of the samples. The mean species richness was 27.6 ± 13.2 OTUs per sample. Thirty-five and 271 OTUs were unique to rock and soil samples, respectively, with a statistically significant difference in mean richness between rocks and soils (12.2 ± 4.2 and 33.3 ± 10.5 OTUs, respectively; Figure S1a). Richness was consistently lower in rocks than in soils at each of the three sites (Figure S1c). At the taxonomic level, 122 OTUs were not assigned to any known fungal phylum, and nine different phyla were identified, with Ascomycota and Basidiomycota representing 107 and 64 OTUs, respectively. At a lower taxonomic level, 15 classes and 33 orders were identified among all samples.

The NMDS ordination indicated a clear separation in the composition of the fungal communities in rock and soil samples (Figure 2). The beta-dispersion analysis showed uniform dispersion in both substrates (*F*-value = 0.2959 and *p*-value = 0.7466) and localities (*F*-value = 2.8793 and *p*-value = 0.1032). PERMANOVA indicated that the differences in community composition were significant when considering substrates ($R^2 = 0.161$, *p*-value = 0.001), localities ($R^2 = 0.098$, *p*-value = 0.002), and the interaction between these two factors ($R^2 = 0.098$, *p*-value = 0.001). However, the analyses showed no statistically significant changes in the richness and Shannon diversity (Figure S1a, b) or the composition of soil fungal communities at increasing distances from rock outcrops (*p*-value >0.05; Figure 2).

The LDA indicated that the differences observed in fungal community composition between rocks and soils were driven by the differential abundance of a large number of OTUs assigned to a few genera. In particular, comparing rock and soil samples from all localities, 40 taxa that were enriched in rock were mainly assigned to lichen-forming fungi in the Lecanoromycetes, with OTUs resolved at the genus level being assigned to *Buellia*, *Lecidea*, *Carbonea*, *Pleopsidium*, and *Lecanora* (Figure 3; Table S1). Additionally, two other taxa enriched in rock samples belonged to the Acarosporaceae and the genus *Friedmanniomyces* (Dothideomycetes) (Figure 3; Table S1). In contrast, 65 taxa that were more abundant in soils than in rocks mainly belonged to yeast taxa, such as the genera *Trichosporon*, *Naganishia*, and *Meyerozyma*, and to the black yeast-like genus *Cryomyces* (Dothideomycetes) (Figure 3; Table S1). The ascomycete genus *Aspergillus* (Trichocomaceae) and five other unclassified taxa, including unidentified members of the *Chytridiomycota*,

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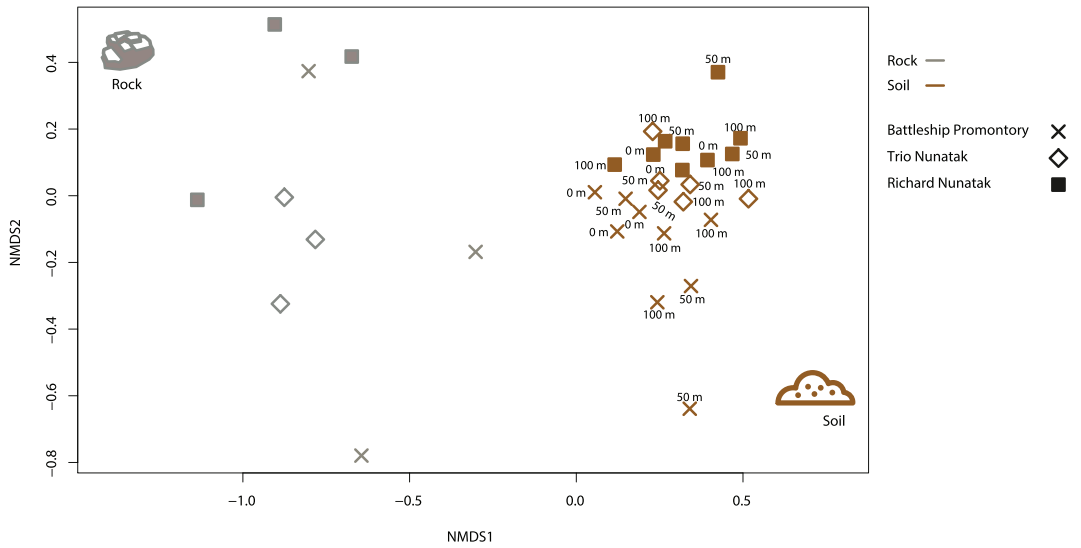

FIGURE 2 NMDS ordination of fungal community composition (Bray–Curtis dissimilarities) in rock and soil samples at three sites in Victoria Land. For soil samples, the increasing distance from rocks in the different sampling sites is reported.

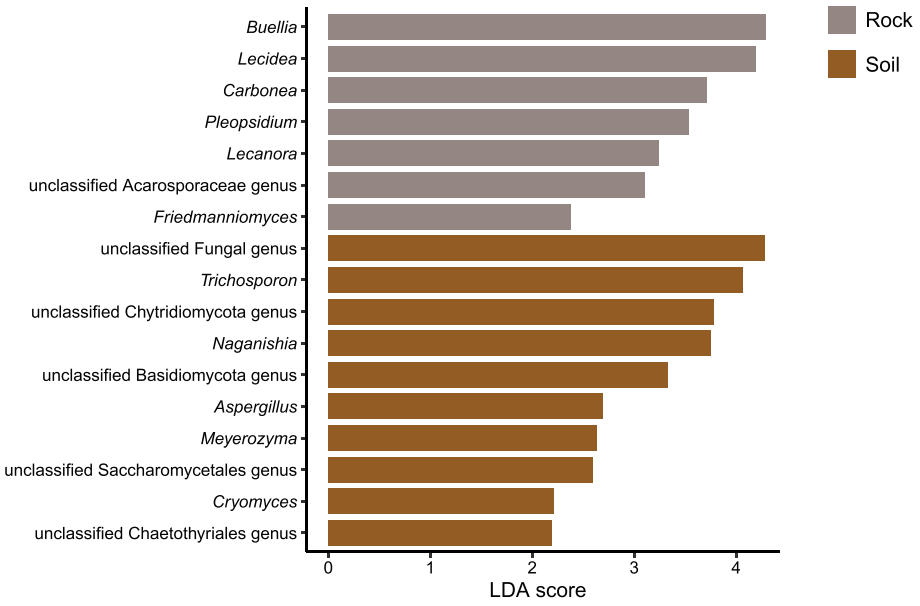

FIGURE 3 Differential abundances of fungal genera between rock and soil samples determined by the linear discriminant analysis (LDA) effect size (LEfSe) method.

Basidiomycota, *Saccharomycetales*, and *Chaetothyriales*, were more abundant in soil than in rocks (Figure 3, Table S1). A similar trend was recorded when differentially abundant taxa at the three localities were examined separately (Table S1). At Richard Nunatak, the taxa that were significantly enriched in rocks compared to soil all belonged to the Lecanoromycetes, and included the genera listed above, and at Battleship Promontory, rocks were also enriched in taxa mainly assigned to lichen-forming fungi. In addition, the genus *Vermiconia* (Dothideomycetes) was significantly more abundant in rock than in soil samples at Battleship Promontory. It was not possible to define differentially abundant taxa between the two substrates at Trio Nunatak.

The CLAM test indicated that 21 and 175 OTUs were restricted to rocks and soils, respectively, and that only three generalist OTUs were characteristic of both substrates (Figure 4; Table S2). One of these generalist OTUs was a member of the Extremaceae, whereas the other two could not be identified below the kingdom level.

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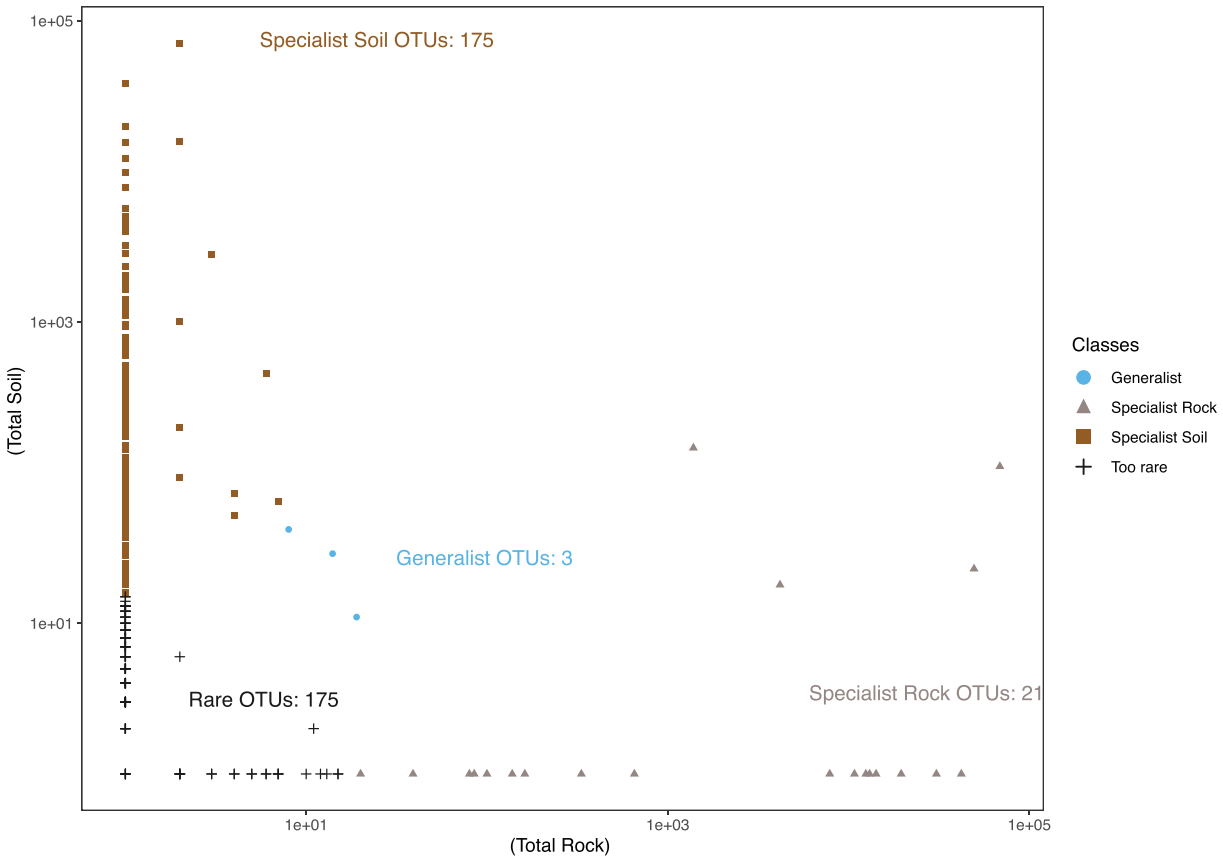

FIGURE 4 Biplot showing the results of the CLAM test based on pairwise comparisons. Generalist, soil specialist, and rock specialist OTUs are shown in blue, brown, and grey, respectively. Rare OTUs are shown in black.

PCA was used to assess how soil samples from different locations were separated based on their physicochemical properties (Table S3; Figure S2). The first two components explained about 70% of the observed variance, with a separation of the samples from the three localities in the first component. The main parameters contributing to the differentiation along the first component were the concentrations of C, N, Mg^{2+}, and Ca^{2+} in soil and the relative abundances of two texture categories (fine silt and sand; Table S4). Correlations between the abundances of the 20 most frequent taxa in the soil samples and physicochemical parameters were significant for four OTUs (Figure 5). Two of these OTUs (OTU105 and OTU4) were identified only as fungi. The abundance of OTU105 was positively associated with the C/N ratio, whilst that of OTU4 was negatively associated with soil C concentration and the percentage of fine silt (Figure 5). The abundance of OTU15, which was assigned to *Naganishia* spp. at 99.6% identity, was positively associated with soil Mg^{2+} concentration (Figure 5). That of OTU29, which was assigned to *Meyerozyma* sp. at 100% identity, was positively associated with concentrations of soil Mg^{2+}, Ca^{2+}, and N (Figure 5).

DISCUSSION

In the present study, we compared the diversity and composition of fungal communities inhabiting rocks and nearby soils in the permanently or seasonally ice-free hyper-arid deserts of Victoria Land. In confirmation of our hypothesis, rocks and soils were strongly selected for different fungal taxa, with the two substrates selecting predominantly for lichen-forming fungi and yeasts, respectively. As in previous studies (Canini et al., 2020, 2021; Pudasaini et al., 2017; Wei et al., 2016), we found both substrates to be characterised by very low fungal diversity, with, on average, 28 fungal taxa being present in each sample, suggesting that only a few taxa are adapted to local conditions and can persist in these harsh environments. Cosmopolitan soil fungal taxa, such as *Aspergillus* spp. (Cox et al., 2019) were infrequent, possibly owing to the remoteness of the sites studied and the limited intercontinental dispersal of some fungi (Archer et al., 2019). Despite rocks providing suitable habitats for microbial growth (Friedmann, 1982; Nienow & Friedmann, 1993), and being thought to host the highest biomass of any substrates in Antarctic terrestrial environments (Cary et al., 2010; Cowan et al., 2014; Cowan & Tow, 2004), fungal diversity was lower in

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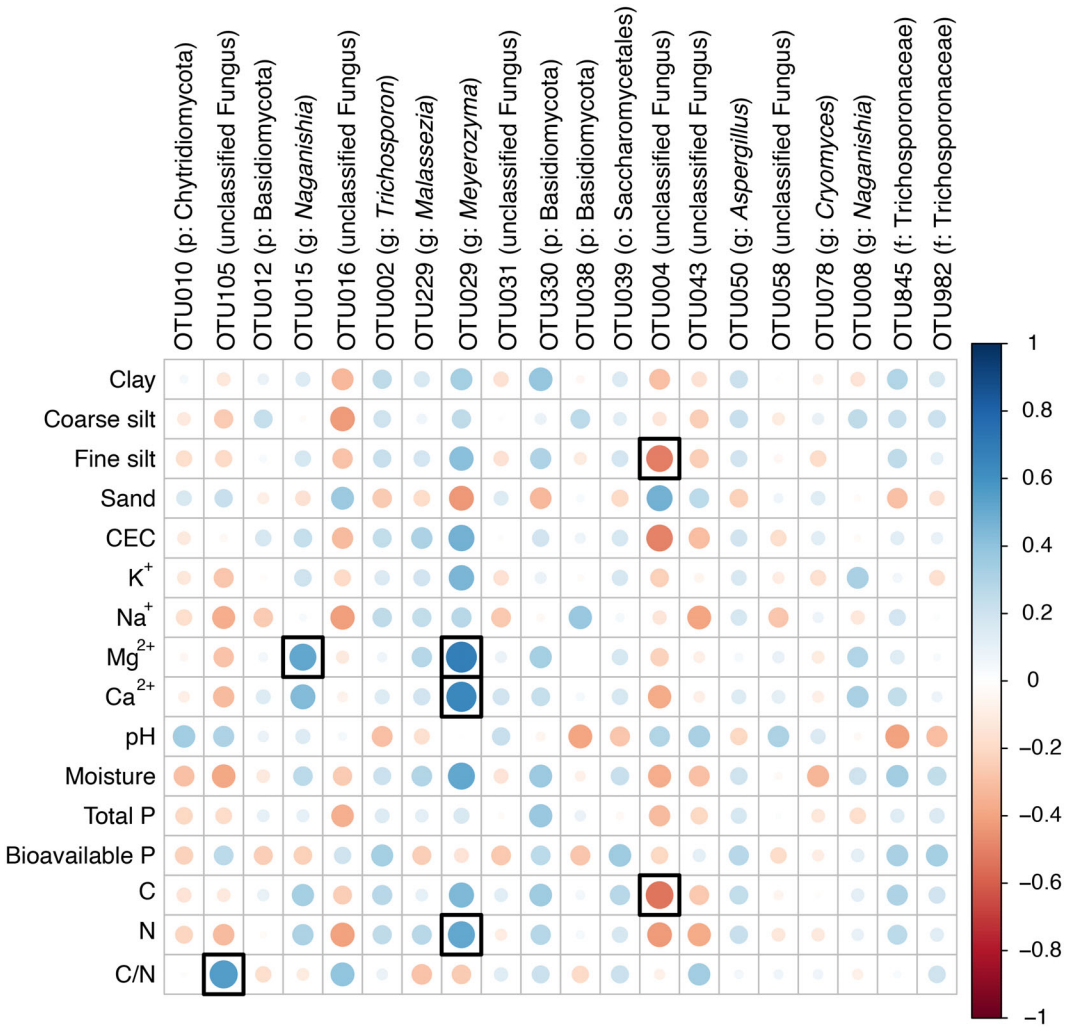

FIGURE 5 The plot of coefficients from Pearson correlations between soil parameters and the abundance of the 20 most frequent OTUs recorded in soil. The colours and sizes of the circles denote the signs and the levels of significance of the correlations, respectively. Squares indicate significant correlations (*p*-values <0.05).

rocks than in soils, with an average of 12 and 33 fungal taxa present in each substrate, respectively. Our results corroborate previous studies showing lower prokaryotic diversity in rocks than in soils of the McMurdo Dry Valleys and Maritime Antarctica (Canini et al., 2023 under review; Garrido-Benavent et al., 2020; van Goethem et al., 2016).

The reasons for the lower diversity of fungal communities in rocks than in soils are still unclear. It is possible that differences in the thermal properties of the two substrates in temperature, which is associated with fungal diversity in Antarctica (Newsham et al., 2021, 2022), might explain the lower number of fungal taxa in rocks. Although continuous monitoring of rock, soil, and air temperatures at Battleship Promontory, Trio Nunatak and Richard Nunatak indicate that average rock temperatures in January exceed those in soil and air at all three locations, the temperatures of rocks fall below those of soils at night, particularly at Battleship Promontory and Trio Nunatak, and rocks thus experience up to 10°C wider diurnal fluctuations in temperature than soils (Table S5). It is thus apparent from these observations that sandstone in the McMurdo Dry Valleys may not provide a more thermally stable habitat than soil, perhaps accounting for the lower diversity of fungi present in cryptoendolithic communities. Further studies are needed to identify whether biologically available water, a strong determinant of fungal species richness (Tedersoo et al., 2014), is similarly more variable in the rocks of Victoria Land than in surrounding soils, and might hence provide further explanation for the lower fungal diversity recorded in the former substrate. Furthermore, soils are a more open environment than rocks, and can therefore receive wind-transported propagules that may increase their diversity. Although it has been shown that relic extracellular DNA persists in soil and inflates microbial diversity estimates (Carini et al., 2016), we do not anticipate that the

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comparatively high diversity of fungi in soil recorded here is associated with the accumulation of DNA in the substrate, since recent research at the three sites studied here shows bacterial diversity to remain higher in soils than in rocks following extracellular DNA depletion (Canini et al., 2023 under review). Despite the higher diversity of fungi in soils than in rocks, soil fungal diversity recorded here is significantly lower than that reported in other studies on continental Antarctic environments, such as those in coastal areas, where milder climatic conditions allow the presence of more diverse fungal communities (Canini et al., 2020; Ji et al., 2016; Siciliano et al., 2014).

Lichen-forming fungi have for decades been widely recognised as the dominant component of Antarctic endolithic communities (Friedmann, 1982), with all of the lichenized genera reported here, such as *Lecanora*, *Buellia*, and *Lecidea*, being more abundant in rock than in soil samples. These genera include species endemic to continental Antarctica, such as *Lecanora fuscobrunnea* (Ruprecht et al., 2012), *Buellia frigida*, and *Lecidea cancriformis* (Ovstedal & Smith, 2001). A dominance of lichens in rocks has similarly been recorded on a glacier forefield in the less extreme environment of Maritime Antarctica (Garrido-Benavent et al., 2020), confirming the specific selective pressure of the substrate for this microbial group. Endolithic lichens adopt a different growth form and lifestyle in rocks compared with their corresponding epilithic forms (Friedmann, 1982). They are particularly well adapted to endolithic growth due to their minimal nutrient requirements, resistance to freezing (Kappen, 2000), and ability to photosynthesize at low temperatures, with minimum temperatures for net photosynthesis of between −6 and − 8°C and optimal temperatures of 1–9°C (Lange & Kappen, 1972; Kappen & Friedmann, 1983).

The soil fungal communities at the three sites studied here were rich in yeasts and yeast-like fungi, notably the genera *Naganishia* and *Trichosporon*, the latter of which is known to occur in other McMurdo Dry Valleys soils (Fell et al., 2006). Several studies have shown that the yeast growth form is widely distributed in Antarctic soils and other cold environments (Atlas et al., 1978; Buzzini et al., 2012; Newsham et al., 2021). This is owing to a range of physiological adaptations, such as the capacity of yeasts to produce polysaccharide capsules, to increase the proportion of unsaturated fatty acids in cell membranes to ensure their fluidity at sub-zero temperatures, and to express cold-active enzymes (Buzzini et al., 2012; Connell et al., 2008; Yusof et al., 2021). In addition, polysaccharide substances exuded by yeast cells promote the formation of soil aggregates by holding soil particles together, improving water and nutrient retention capacity, and enhancing soil properties for microbial colonisation (Pushkareva et al., 2016). Members of Chytridiomycota were also found to be more abundant in soils than in rocks. The Chytrids, a group of flagellated basal fungi, have similarly been shown to occur in soils close to ephemeral streams and ponds in the Antarctic Dry Valleys and maritime Antarctica (Bridge & Newsham, 2009; Canini et al., 2021; Rojas-Jimenez et al., 2017), and, more widely, in aquatic habitats worldwide (Grossart et al., 2016).

Several fungal species endemic to Antarctica, recognised for their remarkable adaptations, belong to the so-called 'black meristematic fungi' (BMF) group. Many of these species have been described from endolithic environments (Selbmann et al., 2005), including members of the genus *Friedmanniomyces*, one of the more commonly reported BMF found using culturing and DNA-based techniques (Onofri et al., 1999; Selbmann et al., 2015a). In agreement with these findings, this genus was more abundant in rocks than in soil in the study reported here. In contrast, the genus *Cryomyces*, previously reported to be a common rock colonist (Onofri et al., 2007), was found to be more abundant in soils than in rocks. Other molecular studies have similarly revealed the presence of this genus in soils (Canini et al., 2021; Czechowski et al., 2016), suggesting that it could be among a small number of resilient taxa that are frequently found in rocks but which also survive in soils. *Cryomyces antarcticus*, which shows remarkable resistance to salinity, desiccation, toxic compounds, and ionising radiation (Aureli et al., 2020, 2023; Onofri et al., 2007; Pacelli et al., 2017b, 2018), survives extraterrestrial exposure in low Earth orbit (Onofri et al., 2019), and *Cryomyces* and other black yeasts are thus considered to be model organisms for studies investigating the lifeforms that might be able to colonise planets with characteristics similar to hyper-arid Antarctic deserts, such as Mars (Selbmann et al., 2015b, Zucconi, et al., 2015; Simões et al., 2023).

As found in other studies (e.g., Chong et al., 2012; Smith et al., 2010; Zhang et al., 2020), the analyses here demonstrated the importance of soil physicochemical parameters in determining the abundances of fungal OTUs in Antarctic soils. Interestingly, in addition to other abiotic parameters known to determine the abundance of soil fungal taxa in Antarctica, such as soil texture and cation concentrations (Canini et al., 2020, 2021; Connell et al., 2006), soil C and N concentrations also strongly affected the abundances of fungi and, as revealed by the PCA analysis, were discriminant variables separating soil samples. In agreement with studies showing increased abundances of yeasts in nutrient-amended oligotrophic Antarctic soils (Newsham et al., 2022), two genera of yeasts, *Naganishia* and *Meyerozyma*, the main constituents of the soil fungal communities at the three study sites, showed positive correlations with cation concentrations in soil. These data confirm previous studies showing

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soil cation concentrations affect the richness and composition of Antarctic soil fungal communities (Canini et al., 2020). They also corroborate studies indicating that yeasts may have developed strategies to rapidly utilise the low-energy compounds available in these soils (Chan et al., 2013), which possibly originate from microbial mats surrounding ephemeral water bodies (Cowan et al., 2014; Hopkins et al., 2009; Pointing et al., 2009).

Sandstone in the McMurdo Dry Valleys shatters under the influence of freeze–thaw events and microbial growth (bioweathering) and is subsequently dispersed widely throughout the landscape by wind (Campbell & Claridge, 1987), suggesting that rocks may be a source of propagules for the colonisation of soil by microbes (Friedmann, 1982). However, we found strong differentiation in the composition of fungal communities inhabiting rock and soil, with numerous unique taxa in both substrates and only three OTUs, including a member of the Extremaceae, shared between them. We also found no apparent changes to the diversity of soil fungal communities at increasing distances from rock outcrops. This suggests that, despite the possible dispersal of fungi in colonised rock fragments (Friedmann, 1982), strong selective pressures act on the two substrates and select for different fungal species, even in soil samples collected close to rock outcrops.

CONCLUSIONS

Fungal communities in rocks and soils in hyper-arid continental Antarctic deserts showed wide divergence, with rocks being dominated by endemic lichen-forming fungi and soils by yeasts, and with lower fungal diversity being found in rocks than in soils. There is little exchange of microbial propagules between the two substrates, with the occurrence of numerous specialist taxa in rocks and soils and a CLAM test identifying just three out of 328 taxa as generalists. Additionally, the abundance of frequent yeast taxa in soils was correlated with edaphic factors. Our observations suggest that stronger temperature fluctuations in rocks than in soils might be responsible for the lower fungal diversity recorded in the former substrate.

AUTHOR CONTRIBUTIONS

Fabiana Canini: Conceptualization; methodology; formal analysis; investigation; data curation; writing – original draft; visualization. **Luigimaria Borruso:** Methodology; formal analysis; visualization; writing – review and editing. **Kevin K. Newsham:** Writing – review and editing. **Federica D'Alò:** Writing – review and editing. **Luigi P. D'Acqui:** Writing – review and editing; investigation. **Laura Zucconi:** Writing – review and editing; conceptualization; funding acquisition; supervision; project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the NCBI SRA archive at https://www.ncbi.nlm.nih.gov/sra, reference number PRJNA998597.

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